



## A review of the biology and literature of the Gulf Coast Toad (*Incilius nebulifer*), native to Mexico and the United States

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### Abstract

The Gulf Coast Toad (*Incilius nebulifer*) is an abundant and widespread species within its range in the United States and Mexico, so it appears on many faunal checklists and is considered in diverse kinds of research. We review the basic biology, distribution, and published history of this species, identifying only those records and publications referable to *I. nebulifer*, to help researchers identify published works pertaining to *I. nebulifer* rather than *I. valliceps*, with which it formerly was considered to be conspecific.

**Key words:** Amphibia, Anura, Bufonidae, *Incilius nebulifer*, Gulf Coast Toad, Mexico, United States

### Introduction

*Incilius nebulifer* (Girard, 1854; Fig. 1), the Gulf Coast Toad, is an abundant species within its range in the United States and Mexico, appearing in many faunal checklists. It is considered in many ecological studies and is the basis for a large number of other research studies in fields such as physiology. Of especial importance is the large number of dissertations and publications involving *I. nebulifer* and/or *I. valliceps* emanating from the productive laboratory of W. F. Blair at the University of Texas during the 1950s–1960s, all of which are presented under the single taxon *Bufo valliceps*. Mulcahy & Mendelson (2000) removed *I. nebulifer* from the synonymy of the abundant Mesoamerican species *I. valliceps* (Wiegmann 1833), but for the majority their taxonomic histories *I. nebulifer* and *I. valliceps* have been considered conspecific. Further, the two species were variously referenced under the taxon *Bufo valliceps*; Frost *et al.* (2006) removed the taxon *nebulifer* from the genus *Bufo*, and it was eventually placed in the genus *Incilius* by Frost *et al.* (2009). Earlier reviews (e.g., Smith & Taylor 1948; Porter 1970), under the name *Bufo valliceps*, are difficult to interpret because they do not distinguish locality records or references referable specifically to either *I. nebulifer* or *I. valliceps*. All recent reviews (e.g., Dodd 2013; Lemos-Espinal & Smith 2007) are based on political boundaries and thus exclude records and references relevant to much of the wide geographic distribution of *I. nebulifer*. In this contribution we summarize the basic biology of *I. nebulifer*, present every geographic record of which we are aware and in which we have confidence, and summarize the publications referable specifically to *I. nebulifer*, regardless of how the taxonomy appears in the publication, across its entire range in both USA and Mexico.

### *Incilius nebulifer* (Girard, 1854)

Gulf Coast Toad

*Bufo granulosus* Baird & Girard, 1852:173. [Not of Spix, 1824]. Type-locality “between Indianola and San Antonio, Texas” [restricted to “Indianola, Calhoun County, Texas” by Schmidt, 1953:66.]. Holotype (fide Kellogg, 1932), United States

National Museum (USNM) 2595, age and sex unknown, collected by J. H. Clark in 1851, under the direction of survey leader J. D. Graham (not examined by authors) Fouquette & Dubois (2014) rejected the restriction of the type locality, claiming lack of published evidence.

*Bufo nebulifer* Girard, 1854:86, preoccupied by *Bufo granulosus* Spix, 1824

*Bufo nebulifera* Baird, 1859a:44.

*Chilophryne nebulifera* Cope, 1862:358.

*Incilius nebulifer* Cope, 1863:50.

*Bufo valliceps* Peters, 1863:81.

*Bufo nebulifer* Mendelson & Mulcahy, 2000:182

*Cranopsis nebulifer* Frost, Grant, Faivovich, Bain, Haas, Haddad, de Sá, Channing, Wilkinson, Donnellan, Raxworthy, Campbell, Blotto, Moler, Drewes, Lynch, Green & Wheeler, 2006:364.

*Ollotis nebulifer* Frost, Grant & Mendelson, 2006:558.

*Incilius nebulifer* Frost, Mendelson & Pramuk, 2009:418–419.

*Bufo (Incilius) nebulifer* Fouquette & Dubois, 2014:315.

**Nomenclatural history.** This species was originally described as *Bufo granulosus* by Baird & Girard (1852) Girard (1854) provided the replacement name *Bufo nebulifer*; as the original name was preoccupied by *Bufo granulosus* Spix, 1824. Peters (1863) placed *B. nebulifer* in the synonymy of Mesoamerican species *Bufo valliceps* Wiegman, 1833, where it remained until Mulcahy & Mendelson (2000) showed that the two species were distinct. Frost *et al.* (2006a) suggested multiple taxonomic changes among New World bufonids, and referred the taxon *nebulifer* into *Cranopsis* Cope, 1875, which was shown by Frost *et al.* (2006b) to be preoccupied, so the taxon was referred to *Ollotis* Cope, 1875. *Ollotis* was found also to be unavailable, so *nebulifer* was finally referred to *Incilius* Cope, 1863, by Frost *et al.* (2009). Various English-language common names have been applied to this species, including Gulf Coast Toad, Coastal Plain Toad, Mexican Toad, Common Toad, and Nebulous Toad. Crother (2012) suggested the name Gulf Coast Toad, which is adopted here. Liner & Casas-Andreu (2008) suggested the standard Spanish name as *Sapo nebuloso*, but were consistent with Crother (2012) in suggesting the standard English name as Gulf Coast Toad.

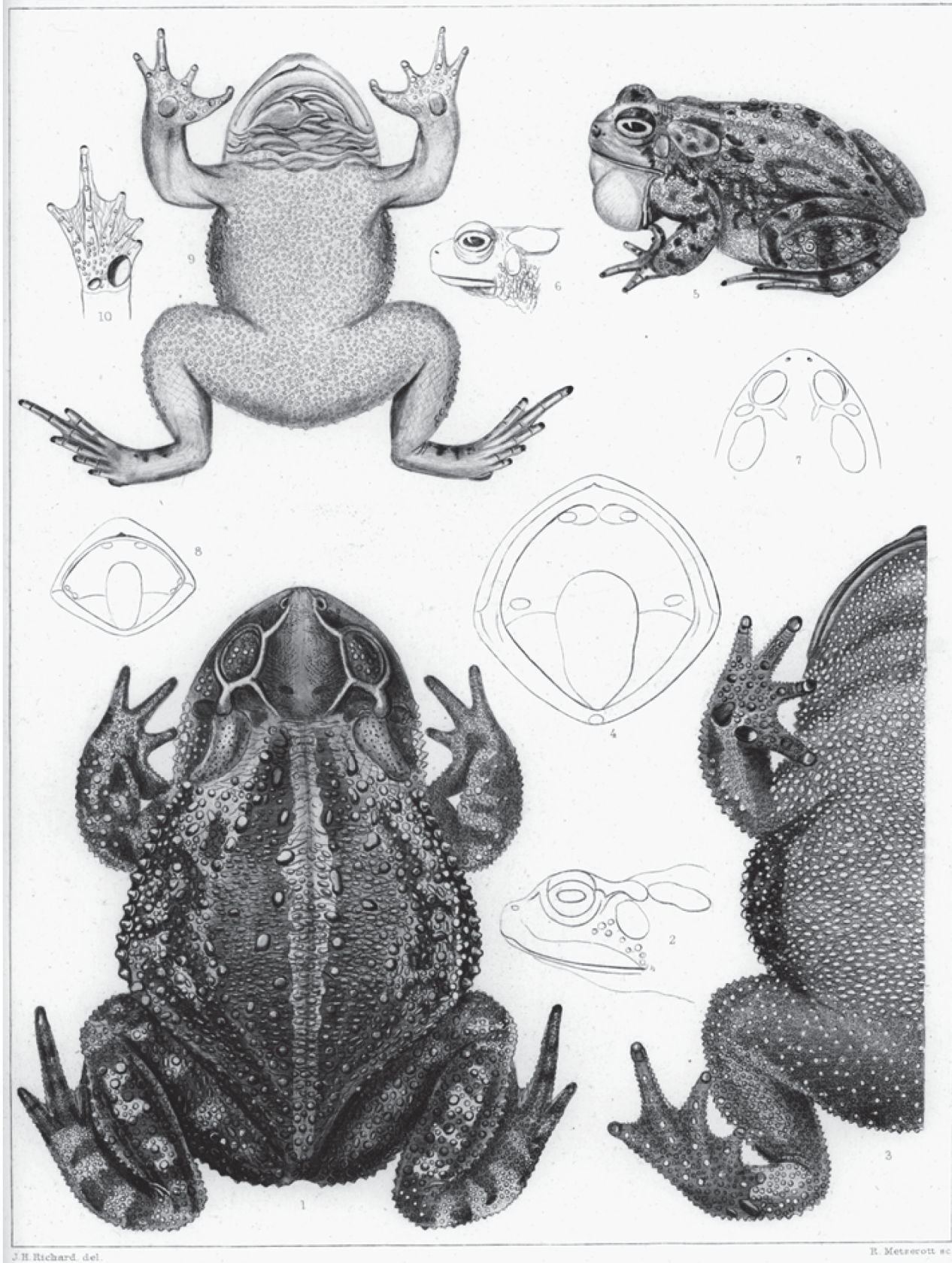
**Definition.** *Incilius nebulifer* is a large toad, with adult females up to 125 mm and males to 98 mm SVL. The head is broad, with a complete complement of low, robust cranial crests. The snout is pointed in dorsal view, and rounded in profile. The tympanum is large (about 50% diameter of the eye). In males, the bilateral vocal slits are large and the *m. interhyoideus* forms a large, bilobed (anteroposteriorly), pigmented vocal sac that may be visible through the overlying gular skin. The skin is uniformly rough, with many evenly distributed sharply pointed tubercles. On the flanks a conspicuous lateral descending row of enlarged sharply pointed tubercles is evident. The ventral surfaces are granular, with unpointed tubercles. Ventral surfaces are usually uniform cream in color while dorsal surfaces are variable. In most individuals the dorsal pattern clearly shows a dark brown dorsal and dorsolateral background coloration, with a broad cream or yellow mid-dorsal stripe and paired dorsolateral stripes (usually ventral to the lateral row of tubercles) of a similar pale color. Variable pale brown or cream markings may be present, scattered across all dorsal surfaces. The tips of the digits are the same color as the remainder of the digit. The hands have short, robust fingers and lack webbing. The feet are long, with slender toes, being about half-webbed.

The larvae are small (attaining 20–25 mm total length) and appear, without magnification, to be nearly uniformly dark gray dorsally, with a series of conspicuous pale spots extending down the dorsal ridge of the tail. The caudal fins are tall and transparent, with some scattered melanophores and iridiophores. The ventrolateral surfaces and the ventral half of the caudal musculature are dark gray with densely distributed silvery iridiophores. The oral disc and the marginal papillae are small and the tooth row formula is 2(2)/3; the A-2 gap is broad, being about one third the length of the A-2 row. The beak is small and shallowly notched.

Advertisement call has a mean frequency of 1479–1785 and a mean pulse of 33.14–38.17 (corrected to 25°C; Porter 1964a).

**Diagnosis.** A large species of *Incilius* (males to 98 mm SVL, females to 125 mm SVL) with the full complement of cranial crests (canthal, supraorbital, supratympanic, postorbital, parietal, preorbital, pretympanic, and suborbital), none of which are hypertrophied to any considerable degree. The tympanum is large (about 50% diameter of the eye), and usually in contact with the pretympanic crest. The skin is rough, with many evenly distributed sharply pointed tubercles over all dorsal surfaces, and with a distinct lateral descending row of enlarged sharply pointed tubercles on the flanks. Tibial glands are absent. The vocal slits are large and bilateral. The parotoid glands are distinctly triangular or subtriangular in shape. The color pattern is remarkably invariable, with





**FIGURE 1.** A reprint of an engraving of *Incilius nebulifer* (original labelled as *Bufo nebulifer*) From Baird, S. F., 1859. Reptiles of the boundary. With notes by the naturalists of the Survey. Imprint: [Washington : s.n., 1859]. plate XL (40) called *Bufo nebulifer*, Grd. Figs. 1–4.





**FIGURE 2.** *Incilius nebulifer*, in life. An adult male photographed in the wild in Harris County, Texas, USA, by Matthijs Hollanders.



**FIGURE 3.** *Incilius nebulifer*, in life. A larval tadpole; image reproduced from Altig *et al.* (1998).

most individuals having dark brown dorsal and dorsolateral background coloration, with a broad cream or yellow mid-dorsal stripe and paired dorsolateral stripes (usually ventral to the lateral row of tubercles) of a similar pale color. No individuals show a distinctive “dead leaf” color pattern dorsally. The tips of the digits are of a similar color to the rest of the digit.

*Incilus nebulifer* is similar in appearance to *I. valliceps* from which it most easily is distinguished by having the dorsal coloration described above (Fig. 2), which is virtually absent in the otherwise polymorphic *I. valliceps*. The two species are parapatric about a geographic line crossing the Gulf Versant of Veracruz, Mexico, near the town of Palma Sola (Mulcahy *et al.* 2006). The tadpoles of *I. nebulifer* (Fig. 3) and *I. valliceps* are essentially indistinguishable, fitting the characters presented in the keys presented by Altig (1970), Altig *et al.* (1998), and

Mendelson *et al.* (1999)—all presented under the taxon *Bufo valliceps*. Hybridization between these two species has not been documented.

**Descriptions.** The original description, as *Bufo granulosus* by Baird & Girard (1852) provided perfunctory details focusing on the cranial crests and coloration. The subsequent taxonomic note (Girard 1854), replacing the preoccupied name *granulosus* with *Bufo nebulifer*, provided no additional morphological descriptions. Baird (1859) also presented a brief description. Cope (1889, as *B. valliceps*) provided a description that is consistent with that of *I. nebulifer* (rather than *I. valliceps*) and indeed it appears to be based mostly on material that is geographically referable to *I. nebulifer*; references to specimens therein that geographically are referable to *I. valliceps* are limited to the “Varieties” section of the account. Kellogg’s (1932, as *B. valliceps*) description is a composite representing specimens referable to both *I. nebulifer* and *I. valliceps*. Descriptions referable to *I. nebulifer* may be found in the following publications: Wright & Wright (1938; 1949; both as *B. valliceps*); Blair *et al.* (1957, as *B. valliceps*), Conant (1958; 1975; both as *B. valliceps*); Dickerson (1969, as *B. valliceps*), Cochran & Goin (1979), Smith (1978, as *B. valliceps*); Behler & King (1979, as *B. valliceps*); Garrett & Barker (1987, as *B. valliceps*); Branson (1995, as *B. valliceps*), Dundee *et al.* (1989, as *B. valliceps*); Conant & Collins (1998, as *B. valliceps*); Trauth *et al.* (2004, as *B. nebulifer*), Lemos-Espinal & Smith (2007, as *B. nebulifer*), Dorcas & Gibbons (2008, as *B. nebulifer*); Elliott, Gerhardt, & Davidson (2009, as *B. nebulifer/Ollotis nebulifer*), Oliver-López *et al.* (2009, as *Ollotis nebulifer*), Tipton *et al.* (2012), and Lemos-Epinal & Dixon (2013). Descriptions of metamorphic and juvenile individuals were provided by Greuter (2004). Descriptions of the tadpole (as *B. valliceps*) were presented by Wright (1929) and, in the form of dichotomous keys, were presented by Altig (1970), Altig *et al.* (1998), and Dodd (2013); Limbaugh & Volpe (1957) and Gosner (1960) described the tadpole through early development. Chromosomal information was presented by Cole *et al.* (1968), Bachman (1970), and Beck & Mahan (1979).

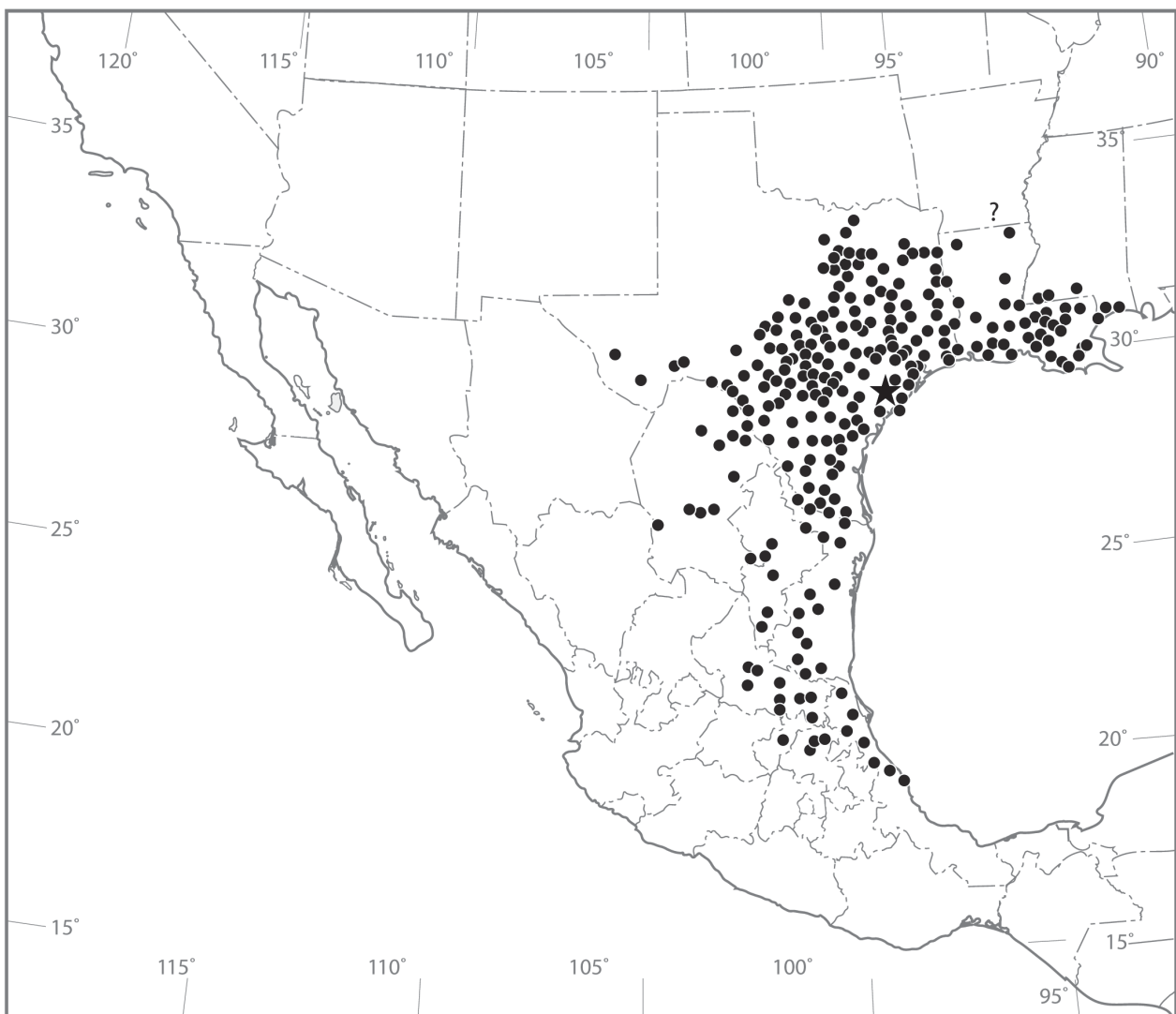
**Illustrations.** Illustrations appear in all of the references cited in “Descriptions” above except that of Baird & Girard (1852). The illustration in Cope (1889) is referable to *I. nebulifer*. Others published illustrations include Cochran (1961, as *B. valliceps*), Clark (1971, as *B. valliceps*), Blair (1972, as *B. valliceps*), Mattison (2007, as *B. nebulifer* and Waddle (2011, as *I. nebulifer*). Illustrations of several osteological elements, based on un-vouchered specimens(s) from San Luis Potosi, Mexico, were presented by Holman (2003). The drawing presented by Powell *et al.* (1998:fig. 58; as *B. valliceps*) is intended to refer to populations in USA (i.e., *I. nebulifer*) but in fact represents the Neotropical species *I. campbelli*; Lemos-Espinal & Dixon (2013:fig. 6) reprinted the same image to represent *I. nebulifer*.

**Fossil Record.** Holman (2003) reviewed published accounts of fossils referred to *B. cf. valliceps* and *B. valliceps* from Scurry County and Culberson County, Texas, USA, respectively. Both records are presumed to be referable to *I. nebulifer*, though both are extralimital with respect to the modern range of the species. The Scurry County record is from the Pliocene, and the Culberson County record is from the Pleistocene. Mulcahy & Mendelson (2000) posited a Miocene–Pliocene vicariant speciation event separating *I. nebulifer* and *I. valliceps* along the Caribbean Coast of modern-day Veracruz, Mexico, with subsequent Pleistocene dispersal of *I. nebulifer* northward into modern-day USA. This hypothesis is not entirely consistent with the fossil records from western Texas, USA. Holman (2003) in his review of North American anuran fossils states definitively the only fossil record of *I. valliceps* (= presumably *I. nebulifer*) is from Fowlkes Cave, Culberson County, Texas; thus he casts doubt on the validity of the Pliocene record from Scurry County, Texas.

**Remarks.** The town of Indianola, referenced in the type locality, no longer is recognized after being decimated by a series of hurricanes in the 1800s. It was located near the mouth of Matagorda Bay on the Gulf Coast of Calhoun County, Texas, USA, at approximately N 28° 30’, W 96° 29’. Despite the initial taxonomic misstep by Baird & Girard (1852) and the recent taxonomic changes of generic names for the clade of Mesoamerican bufonids (Frost *et al.* 2006a; 2006b; 2009), the species was referred consistently to as *B. valliceps* in all literature and taxonomic checklists (e.g., Gorham 1974) from the time of Cope (1863) until Mulcahy & Mendelson (2000). Consequently, the literature on this species is relatively simple to search and interpret, so long as the reader can determine the provenance of the material being discussed (i.e., USA and northern Mexico vs. southern Mexico and Central America). With this distinction in mind, the majority of the literature relating to ecology, behavior, and physiology that was published under the name *Incilius* (= *Bufo*) *valliceps* actually pertains to *I. nebulifer*. Note that Trauth *et al.* (2004) incorrectly listed Mulcahy & Mendelson as the authority for the taxon *nebulifer* when, in fact, it is Girard.

**Etymology.** The name *nebulifer* is derived from *nebula*, meaning “cloud” and “fer” meaning “bearing” and is in reference to the generally clouded color pattern of this species. The etymology provided by Dodd (2013), for the taxon *nebulifer*, is incorrect.

**Distribution.** We present a map of locality records in Fig. 4. Consideration of the distribution of *I. nebulifer* suggests that it is limited at its southern extent by the seemingly minimal eastern tail of the Trans-Mexican Volcanic Axis (Mulcahy *et al.* 2006), whereas it appears to be capitalizing upon human habitat disturbance and actively expanding its distribution eastward in the United States (Vogel and Pechman 2010; Milko 2012). Presumably, the northern distributional limit is delimited by winter temperatures, although the species does occur in areas known to experience hard freezes. Similarly, it appears that the western distributional limits are contained by the cooler conditions on the uplift of the Sierra Madre Oriental in Mexico. In USA and extreme northern Mexico, the distributional pattern appears to follow permanent drainages in the Chihuahuan Desert, suggesting that aridity plays a factor in delimiting the range in this area. However, none of these hypotheses regarding physiological effects of low temperatures and dryness as factors limiting the distribution have been explicitly tested.



**MAP.** The distribution of *Incilius nebulifer*. Dots indicate locality records. The approximate location of the type locality is indicated with a star. Question mark indicates a valid specimen record that likely does not represent a natural, nor established, population (see text).

Distributional notes were presented by Hallowell (1856), Baird (1859), Garman (1887), Cope (1888), Strecker (1902), Stone (1903), Gadow (1905), Strecker (1908a,b; 1909; 1926a–d), Sanders (1909), Strecker (1926a–c),



Strecker & Williams (1927), Strecker (1928), Burt & Burt (1929), Strecker (1930), Burt (1935), Strecker & Johnson (1935), Schmidt & Owens (1944), Smith & Buechner (1947), Smith (1948), Blair (1950), Brown (1950), Milstead *et al.* (1950), Peterson (1950), Reese & Firschein (1950), Anderson *et al.* (1952), Smith & Sanders (1952), Raun (1959), Milstead (1960), Webb & Packer (1961), Lewis (1974), Conant (1977), Carl (1980), Rackowitz *et al.* (1983), Thornton & Smith (1993), Blair *et al.* (1995), McAllister & Ward (1986), Fleet & Aubrey (1997), Ramírez-Bautista (1999), Dixon (2000), Dayton *et al.* (2001), Johnson (2002), Gifford & Fontenot (2003), Hibbitts *et al.* (2008), Price (2009), Lazcano *et al.* (2012), Dixon & Hibbitts (2013), Farr *et al.* (2013), and Maxwell (2013).

Although this species is listed in most literature and field guides (e.g., Conant & Collins 1998; Dorcas & Gibbons 2008) as occurring in the state of Arkansas, USA, Trauth *et al.* (2004) reported that the occurrence in that state is based on but a single record (first reported by Smith & Langebartel (1949) near Calion, Union County, Arkansas; no additional records have been found. While Trauth *et al.* (2004) continued to list the species as part of the fauna of Arkansas, it seems unlikely that a viable population ever existed within the boundaries of Arkansas; that record is indicated on the map herein, but is not considered as part of the natural range of the species. A geographically proximal record, from Morehouse Parish, Louisiana, USA, is based on a specimen in the University of Louisiana at Monroe (ULM 16976) and does appear to be properly identified (J. L. Carr, pers. comm.); we have no information to discredit the validity of its locality data. However, we agree with J. Boundy (pers. comm.) that the natural northern boundary of *I. nebulifer* in Louisiana appears to lie in the lower Red River Valley, in Rapides Parish. The locality mapped by Dundee *et al.* (1989) for Richland Parish is not based on an extant voucher specimen (J. Boundy, pers. comm.); so, we do not include that record here. Given the proximity of Caddo Parish, in northwestern Louisiana, to known records in adjacent counties in northeastern Texas gives us a somewhat objective reason to predict the presence of the species in northeastern Texas, despite the apparent lack of records. Specimens mapped from Jones County, Mississippi, USA (Mendelson, *in* Lannoo 2005) are based on specimens at the University of Southern Mississippi that have highly suspect locality data (R. L. Jones, pers. comm.); based on this information, we discount records from that county.

In the western extreme of its distribution, in the Chihuahuan Desert, *I. nebulifer* appears to be restricted to the primary watercourses draining into either basins or into the Rio Grande that forms the US–Mexican border. In Mexico, Lemos-Espinal *et al.* (2004) do not list this species, under any taxonomic name from the State of Chihuahua; based on records of species in drainages into the Rio Grande in Texas, USA, we suspect this species will be found in similar drainages in Chihuahua, Mexico. Espino de Castillo *et al.* (2009) mention a toad they refer to *Incilius valliceps* from Los Riscos cave, in the State of Querétaro, but with no mention of voucher specimens; we do not include this record on the map presented here.

**Biology of The Gulf Coast Toad.** The catalogue account for *Bufo valliceps* (Porter, 1970), as well as Porter's (1962; 1964a–c) overall concept of the species, is a composite of *I. nebulifer*, *I. valliceps*, and additional species of *Incilius* (Mendelson 1998); however, those records and literature cited that pertain to specimens from the currently known range of *I. nebulifer* are valid for this latter species.

**Morphology.** Morphological descriptions and analyses of morphological data were presented by Bauldauf (1958), McAlister (1961), W. Martin (1967; 1971), R. Martin (1972a,b), Martin & Gans (1972), Gans (1973), Emerson (1982), Hutchinson & Savitzky (2004) R. Martin (1972b). The analyses of sternal morphology and inguinal fat body organs by da Silva & Mendelson (1999) included specimens referable both to *I. nebulifer* and *I. valliceps*, however no differences in these structures are evident between the two species (Mendelson *et al.* 2011). The osteological review provided by Martin (1973) is problematic because it was based on specimens referable to *I. nebulifer*, but also included a skeletal specimen identified as *Bufo valliceps* (the specimen in Martin 1973:fig. 2D is TNHC 41994; T. LaDuc, *in litt.*); this specimen bears the locality data “Mexico: Sinaloa” which is greatly extralimital for the either *I. nebulifer* or *I. valliceps*. Blair (1962; 1970) discussed the importance of various types of data to inform understanding of this species, with respect to other bufonids. Cytological comparisons with other bufonid species were presented by Sanders & Cross (1964). A morphologically anomalous specimen was described by Freed (1992) and larval deformities by Drake *et al.* (2007). Effects of long-term preservation on specimens were reported by Deichmann *et al.* (2009).

**Reproduction, development, and hybridization.** Various aspects of the reproductive biology, including the advertisement calls, of *I. nebulifer* have been documented by A. P. Blair (1947), Wright & Wright (1949), Duran (1954), Martin (1958), W. F. Blair (1956a; 1960a), Thornton (1960), Awbrey (1963), Porter (1964a), Hubbs &

Martin (1967), Grubb (1970, 1973a), W. Martin (1972), Wiest (1982), Sullivan & Wagner (1988), Dundee *et al.* (1989), Ryan & Sullivan (1989), Branson (1995), Wagner & Sullivan (1992; 1995), Foley (1994), Greuter (2004), Lannoo *et al.* (2005), Salinas (2009), Jones & Ratnam (2009), Pierce & Hall (2012), and Oyervides & Zaidan (2013). Development, metamorphosis, and ontogeny and factors affecting them have been documented by Taylor (1942), Wright & Wright (1949), Volpe (1957), Limbaugh (1956), Limbaugh & Volpe (1957), Conant (1958, 1975); Blair (1953; 1956b; 1960a; 1963), Turner (1960, 1962), Hubbs *et al.* (1963), Ballinger & McKinney (1966), Yew (1966; 1969), Licht (1967), Grubb (1973b), Dundee *et al.* (1989), Pierce & Montgomery (1989), Nelson (1993), Rosenberg (1990), Rosenberg & Pierce (1995), and Conant & Collins (1998). Various aspects of hybridization with other anurans have been discussed by Blair (1941), Orton (1951), Liner (1954), Thornton (1954, 1955), A. P. Blair (1941), W. G. Blair (1956b; 1958; 1959; 1960a; 1961b; 1963; 1964; 1966; 1972), Moore (1955), Volpe (1956; 1959; 1960), Gosner & Black (1958), Fox *et al.* (1961), Kennedy (1962), Brown (1971a, b), Guttman (1972), Brown & Brownell (1971), Brownell (1971), Sanders (1978; 1985; 1986), Hillis *et al.* (1984), Dundee *et al.* (1989), Greuter (2004), Brown & Mesrobian (2005), Mulcahy *et al.* (2006), and Mendelson *et al.* (2011). This older literature regarding hybridization must be interpreted in the context of the taxonomic separation of *I. nebulifer* and *I. valliceps* by Mulcahy & Mendelson (2000), and also in the context of the re-analyses of data from the laboratory of W. F. Blair presented by (2008) and subsequently re-analyzed by Brandvain *et al.* (2014). Additional, recent, studies of hybridization were presented by Vogel (2007) and Vogel & Johnson (2008).

**Habitat use.** Habitat use by the adults has been discussed by Pope (1919), Wright & Wright (1949), Thornton (1960), Awbrey (1963), Brattstrom (1963), Wilks (1963), Grubb (1968, 1970), Neill & Grubb (1971), Grubb (1976), Moore (1976), Whiting *et al.* (1987), Dundee *et al.* (1989), McAllister *et al.* (1989), Foley (1994), Reid & Whiting (1994), Irwin (1997), Mendelson (1998), Mulcahy & Mendelson (2000), Means (2005), Mulcahy *et al.* (2006), Lemos-Espinal & Smith (2007), Vogel & Johnson (2008), Salinas (2009), Oliver-López *et al.* (2009), Gehlbach (2010), Walls *et al.* (2011), Hernández-Salinas *et al.* (2012), and Milko (2012). Associations with caves has been reported by Mohr (1948), McAlister (1954), Baker (1957), Redell & Knox (1962), Redell & Finch (1963), and Reddell (1970). Specific associations with saltwater were documented by Viosca (1926), Allen (1932), Burger *et al.* (1949), reviewed by Neill (1958), Mueller (1985), Alexander *et al.* (2012) and Hua & Pierce (2013). Responses to fire were reported by Brown *et al.* (2011; 2014). Potential effects of exposure to introduced plant species were reported by Cotton (2009) and Cotten *et al.* (2013).

**Community ecology.** Feeding ecology has been documented by Strecker (1927a), Campbell & Davis (1968), Clark (1969), and McGehee *et al.* (2001). Predators and possible antipredator mechanisms have been documented by Strecker (1927b), Wright & Wright (1949), Licht (1968), Neill (1968a,b), Grubb (1972), Clark (1974), Brown (1974), Platt & Fontenot (1993), Tucker (1994), Adams (2005), and Mendelson (2005). Palatability of the tadpoles was tested by Adams *et al.* (2011). Parasites have been reported by Walton (1929), Harwood (1930), Hoffpauir & Morrison (1966), McAllister *et al.* (1989), McAllister & Donn (1990), and Martin & Dresser (1991). Pathogens were reported by Gaertner *et al.* (2010), and Saenz *et al.* (2010). Interspecific associations with other anurans have been discussed by Glass (1946), Wright & Wright (1949), Axtell (1958), Blair (1961a), James (1966), Moore (1976), Gambs & Littlejohn (1979), Foley (2005), Mitchell & Lannoo (2005a,b), Schwalbe & Goldberg (2005), Franklin & Killpack (2005), Sredl (2005), Sredl & Field (2005), Sullivan (2005), Wallace (2005), Vogel & Pechmann (2010), and Preston *et al.* (2014). Associations with other species caught in traps with this species were reported by Blair (1960b). Population trends were discussed by Boundy (2005). Camper & Dixon (1988) evaluated a microchip marking technology in the species. Road and industrial mortality was reported by Flickinger (1981) and Ray *et al.* (2006); road mortality and scavenging by *Thamnophis proximus* was reported by Watson (2007).

**Physiology and behavior.** Various aspects of the physiological parameters and responses in this species have been presented by Morgan & Stokes (1936), Svedberg & Hedenius (1934), Sanders (1962), Wittliff (1964), Campbell & Davis (1971), Guttman (1974), Withers (1978), Prasad *et al.* (1984), Wygoda (1989), Williams (1992), Williams & Wygoda (1993), Verma & Pierce (1994), Moore (1997), and Rowson *et al.* (2001). Veterinary protocols were presented by Brannelly *et al.* (2012) and Brannelly (2014) and notes on captive care were provided by Walsh *et al.* (1992). Phototactic responses were presented by Jaeger & Hailman (1973) and Hailman & Jaeger (1974); however, the source for the specimens used by Jaeger & Hailman (1973, presented as *B. valliceps*) is not reported, so referral of data as relevant to *I. nebulifer* is speculative. Interspecific effects of injections of pituitary extracts were presented by Quinn & Mengden (1984). Hemoglobins and transferrins were described by Fox *et al.* (1961). Resistance to cardiotoxins was reported by Moore *et al.* (2009) The parotoid secretions were analyzed by



Porter (1964c), but results are based on specimens referable both to *I. nebulifer* and *I. valliceps*. Serological comparisons were made by Durio (1960) and biochemical components in the skin were analyzed by Cei *et al.* (1968). Use of this species for human pregnancy testing was evaluated by Aguirre-Pequeño (1950). Effects of potentially toxic chemicals were evaluated by Chen & Chen (1933), and Shaw & Grushkin (1957). Effects of radiation were reported by Blair (1960c) and Clayton (1960). Clark (1971) reported on use of branding as a means of marking individuals. Greding (1971) reported on learning in this species.

**Evolution.** The phylogenetic literature, with respect to *I. nebulifer*, can be difficult to interpret if the authors did not state the provenance of the samples used in their analyses. For example, Baldauf (1959) implies that the individuals used in his morphological analyses were collected in the USA (and possibly may be the same individuals reported by Baldauf, 1958), but one cannot be certain. Maxson (1984) and Maxson *et al.* (1981) included “*Bufo valliceps*” in their studies from Texas, so they can be assigned with certainty to *I. nebulifer*.

All phylogenetic treatments of the taxon “*valliceps*” published prior to 2000 were based, variously, on specimens or samples representing either *I. valliceps* (sensu stricto) or *I. nebulifer*. The modern reader of those papers is encouraged to check the geographic source of the material included in any particular analysis and assign the appropriate taxonomic name. Because of the well-supported sister-taxon relationship between *I. nebulifer* and *I. valliceps* (Mulcahy & Mendelson 2000; Mulcahy *et al.* 2006; Mendelson *et al.* 2011), the taxonomic differences typically have virtually no bearing on the overall evolutionary discussions presented by those authors. The exception, however, is the result presented by Van Bocxlaer *et al.* (2010), wherein they reported that the species pair *valliceps* + *nebulifer* was rendered paraphyletic by a sample identified as “*I. macrocristata*” (= *I. macrocristatus*). Mendelson *et al.* (2011) reviewed all of the relevant material, presented a clarification of the issue and determined that Van Bocxlaer *et al.* (2010) had included a misidentified specimen in their analyses (i.e., their sample of “*I. macrocristata*” actually represented *I. valliceps*). In their broad analysis of amphibian relationships, Pyron & Wiens (2011) chose to compile various published genetic sequences (i.e., GenBank) to create chimera to represent the taxa “*Bufo valliceps*” and “*Bufo nebulifer*” for their analyses; their compilation of sequences from various sources into singular OTUs included the misidentified material from Van Bocxlaer *et al.* (2010), with the result that Pyron & Wiens presented “*valliceps*” and “*nebulifer*” not to be sister taxa. Because their analyses include clearly misidentified material, this section of their overall phylogenetic tree is inadmissible. Thus, the sister relationship between *I. valliceps* + *I. nebulifer* remains is supported by all modern phylogenetic analyses that are based on accurately identified material. Phylogenetic relationships, biogeographic history, and evolutionary natural history of *I. nebulifer* were presented and discussed by Mulcahy & Mendelson (2000), Mulcahy *et al.* (2006), and Mendelson *et al.* (2011). The relative phylogenetic diversity of *I. nebulifer*, with respect to other North American bufonids, in terms of conservation prioritization was presented and discussed by Goebel (2005).

**Conservation and education.** Summary of possible conservation threats to this species were presented by Hammerson & Canseco-Márquez (2004), Mendelson (2005), Frías-Alvarez *et al.* (2010). Use of habitat by this species following mining activities was reported by Walton (2012). Use of these common toads in conservation-awareness education programs was described by Rommel (2012).

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